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Historical daytime vertical structure of larval fish assemblages in southeast Australian coastal waters: A benchmark for examining regional ecosystem change

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ABSTRACT

Historical data are often used as benchmarks or reference points for assessing regional changes in ecosystem structure and function. For that purpose, we provide historical (1991–1992) data concerning the spatial and temporal consistency of vertical structuring of a diverse assemblage of larval fishes in inner continental shelf waters adjacent to Sydney, Australia. Daytime vertically stratified sampling at seven depths (0–65 m) across four stations and five sampling seasons yielded 35,772 individuals of 94 identifiable taxa from 81 families. Assemblages displayed consistent vertical stratification between surface (0 and 5 m) and subsurface (15 m and deeper) waters, with further spatio-temporal sub-structuring of subsurface assemblages between upper (15–30 m) and lower (45 m and deeper) water column. Differences in assemblage structure between surface and subsurface waters were primarily driven by several species that predominantly occurred in one depth zone and not the other. In contrast, differentiation between subsurface assemblages was dynamic and driven by taxa common across upper and lower subsurface depths but occurring in differing densities in certain depth strata that was spatially and temporally variable and not related to thermal stratification of the water column. Despite significant small-scale spatio-temporal variability, larval taxonomic diversity and total abundance was most often greatest in the upper and mid water column (15–30 m), potentially a response to light levels and prey concentrations. Nevertheless, the data show that all depths in the water column provide important habitat for larval fishes that need to be considered in ecosystem functioning and climate change projections.

1. Introduction

Marine fish larvae display a vast array of vertical distributions that influence their dispersal, transport and supply to juvenile habitats (Norcross and Shaw, 1984; Leis, 1991; Cowen et al., 1993, 2007; Muhling and Beckley, 2007). Knowledge of how larval assemblages are vertically structured in time and space can lead to greater understandings of the mechanisms and processes that influence recruitment dynamics, population fluctuations and ecosystem functioning (Jenkins et al., 1997; Leis and McCormick, 2002; Köster et al., 2003; Abesamis et al., 2016; Koslow and Wright, 2016).

Continental shelf waters world-wide provide habitat for the larvae of numerous ichthyofaunal species, including those of economic and social significance (Olivar and Shelton, 1993; Nonaka et al., 2000; Hernandez-Miranda et al., 2003; Muhling et al., 2008). Such waters are often characterized by high oceanographic complexity and subject to anthropogenic-derived environmental stressors. Subsequently, the vertical and horizontal distributions of a range of coastal fish larvae have been examined in many regions throughout the world, often in association with particular oceanographic features over short time frames (Olivar and Sabates, 1997; Smith and Suthers, 1999; Rodriguez et al., 2006; Borges et al., 2007). Few studies have examined the consistency of vertical structure of ichthyoplankton assemblages across different seasons when larval taxonomic composition and oceanographic conditions often differ (Muhling and Beckley, 2007; Espinosa-Fuentes et al., 2017).

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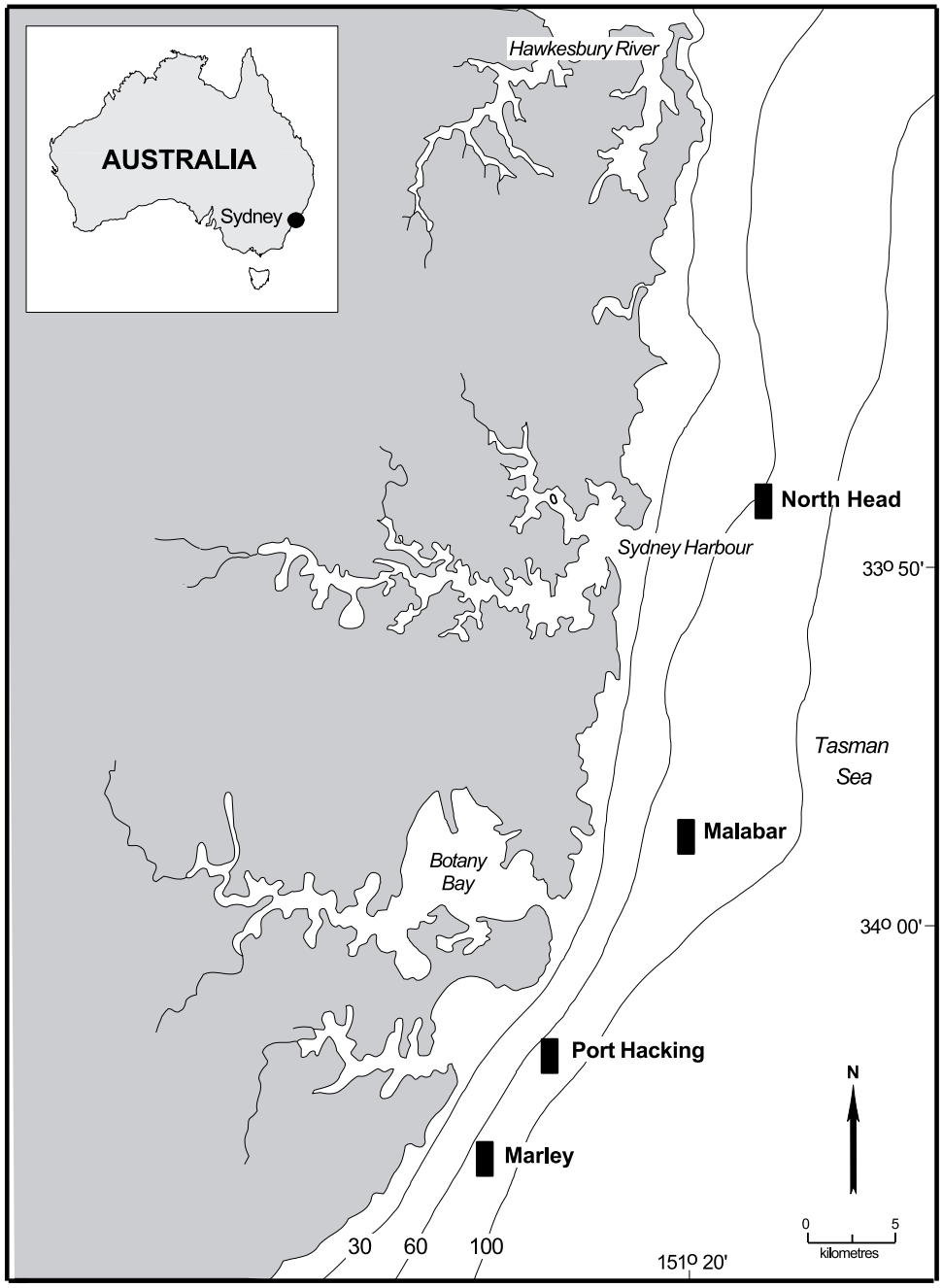

Fig. 1. Map of the Sydney coastal region showing the location of the four sampling stations. The isobaths show depth (m).

Table 1
The month and year, depth stratum sampled, temperature range between surface and bottom waters, the presence and depth of the stratified thermal layer and the total number of larval fish taxa and individuals sampled in each of five sampling times.

Sample	Month and Year	Depths sampled (m)	Temperature range 0–65 m	Thermal stratification	Depth of stratified layer (m)	No. of taxa	No. of individuals
Time 1	February/March 1991	5,15,30,45,55	23.0–15.8 °C	Y	10–55 m	65	1 666
Time 2	October 1991	5,15,30,45,55	17.5–13.5 °C	Y	10–40 m	53	4 360
Time 3	February 1992	0,5,15,30,45,55,65[a]	22.5–16.1 °C	Y	20–60 m	81	21 131
Time 4	August/September 1992	0,5,15,30,45,55,65[a]	16.6–15.5 °C	N	n/a	65	5 836
Time 5	November/December 1992	0,5,15,30,45,55,65[a]	17.2–14.4 °C	Y	10–45 m	66	2 779

[a]65 m samples were not collected at North Head.

Using historical data, this study identifies and compares between seasons the vertical structure of the larval fish assemblages inhabiting inner continental shelf waters of southeastern Australia, a climate-change hot-spot with projected major changes in oceanography and marine ecosystem structure (Hobday and Lough, 2011). Historic and recent studies have distinguished that these temperate waters display marked seasonality in larval fish composition and oceanography (Gray and Miskiewicz, 2000;

Suthers et al., 2011), with distinct larval assemblages associated with seasonal upwelling events, occurrences of particular water masses and eddies, and small- and meso-scale currents (Dempster et al., 1997; Smith et al., 1999; Smith and Suthers, 1999; Gray and Miskiewicz, 2000; Keane and Neira, 2008; Mullaney et al., 2011; Syahailatua et al., 2011; Mullaney and Suthers, 2013; Matis et al., 2014). Complimentary historical vertically stratified sampling has further identified compositional differences between larval fish assemblages in surface and subsurface (20–30 m depth) strata (Gray et al., 1992; Gray, 1993; Gray and Miskiewicz, 2000), but the structure of assemblages and the distributions of individual taxa over finer depth strata throughout the entire water column remain less documented. Sampling over such scales has examined diel changes and relationships of the thermocline on the vertical distributions of common taxa (Gray, 1996a,b, 1998; Gray and Kingsford, 2003). For the vast majority of fish larvae, little has been published concerning seasonality in their vertical distributions and concomitant assemblage structure; such important primary historical information is provided in this paper. These data provide a benchmark for examining regional changes in the vertical structure of larval fish assemblages associated with climate-related environmental impacts.

2. Methods

2.1. Sampling

Larval fish assemblages at four stations situated between the 60 and 80 m depth contours and 2–3 km offshore of Sydney (between North Head — 33.80 °S and Marley Beach — 34.12 °S; Fig. 1) were systematically sampled at specific depths (nominally the surface [= 0 m], 5, 15, 30, 45, 55 and 65 m) across five independent sampling times in 1991–1992 (T1–T5; Table 1). The 80 cm cylindrical/conical sampling nets had 500 μm mesh in the body and 250 μm mesh in the collecting bag and were fitted with messenger-operated open–close mechanisms (General Oceanics DT-1000) to stop contamination of samples upon deployment and retrieval. During each sampling period, three separate five minute horizontal tows were done at each depth at each of the four stations (except 0 and 65 m in T1 and T2, and 65 m at North Head across all seasons). All sampling was done during daylight and each station was sampled on a different day within each sampling time. When possible, the four stations were sampled on consecutive days within each period, except when inclement weather or prior commitments of the research vessel restricted sampling. The order in which each depth was sampled at a station was randomly allocated and it took approximately four hours to complete sampling at each station. Fish larvae from each sample were sorted, identified to the lowest possible taxonomic level using a variety of reference sources, counted and developmental stage (preflexion, flexion and postflexion) determined under a dissecting microscope. Yolk-sac staged larvae were not identified and excluded from analyses.

2.2. Analyses

The numbers of fish larvae in each sample were standardized per 100 m^3 of water filtered and all analyses were performed on log (x+1) transformed data using the PRIMER V6 statistical package (Clarke, 1993; Anderson, 2001). Two-way permutational analyses of variance (PERMANOVA) were used to test for significant differences among depths and stations in the structure of assemblages, numbers of taxa (larval fish diversity) and individuals (abundance) in each sample time. The multivariate (composition) and univariate (diversity, abundance) analyses were based on the Bray–Curtis and Euclidean distance measures, respectively, using 9999 permutations of transformed data (Anderson, 2001). In each analysis depth and station were orthogonal and treated as fixed and random factors, respectively. When the depth or interaction term was significant, subsequent pairwise comparison tests based on the Monte Carlo P value were used to identify statistically significant differences in diversity, abundance or assemblage structure among individual depths at each station.

Assemblage vertical stratification in each sample time was assessed using hierarchical agglomerative clustering and non-metric multidimensional scaling (NMDS) ordination techniques based on the Bray–Curtis similarity measure (Clarke, 1993). The clustering analyses identified linkages among samples and subsequent assemblage groupings within each sample time were categorized at the 40% level (to minimize group numbers). Similarity Percentage Analyses (SIMPER) were used to determine the taxa that contributed greatest to the similarity matrix of the predominant assemblage groupings in each sample time (Clarke, 1993). Likewise, SIMPER was also used to determine the taxa that contributed greatest to the dissimilarity matrix between subsurface assemblages. Representative and typical taxa were those that contributed to the top 50% of the average similarity within an assemblage and had a high average similarity and similarity/standard deviation ratio (Clarke, 1993). The interrelationships among samples as well as each identified assemblage grouping was graphically displayed on two dimensional NMDS ordination plots for each time. Separate NMDS ordinations of only the subsurface samples were done to further assess potential sub-structuring of these assemblages in T3–T5 (see results).

3. Results

3.1. Assemblage diversity and abundance

In total 35,772 individuals of 94 identifiable taxa from 81 families were collected in samples (Supplementary Table 1). The greatest numbers of total taxa (81) and individuals (21131) occurred in T3, and least taxa (53) in T2, and individuals (1666) in T1 (Table 1). Most sampled larvae were pre-flexion: 72.7–88.2% depending on season.

Significant small-scale spatio-temporal variability in depth distributions in the numbers of larval fish taxa and individuals was evident across each sampling time (significant Depth x Station interaction in all 10 Permanovas; $P < 0.001$). Nonetheless, the pairwise comparisons detected some significant and observable patterns; notably, larval diversity was greatest at 15 and 30 m in T2 (except Marley) and T5 (except Malabar), and least at 0 and 5 m in T4 and at 55 and 65 m in T3 (except Malabar) (Fig. 2). There were few notable patterns for mean larval abundance, except that it was greatest at 15 and 30 m in T2 (except Marley) and T4, and between 15 and 45 m in T5 (except Malabar) (Fig. 3).

3.2. Assemblage stratification

The structure of assemblages significantly ($P < 0.001$) varied according to the depth x station interaction in the Permanova analysis for each sampling time. The pairwise comparison tests identified significant differences in assemblage structure between depths at each station within each time, but few global generalizations could be made other than assemblages at 0 and 5 m generally differed to those at deeper depths. Specific differences between depths were dependent on the station and sampling time.

The cluster and ordination analyses identified that assemblages were vertically stratified across all five sampling times with strong assemblage differentiation occurring between surface (0 and 5 m) and subsurface (15 m and deeper) waters

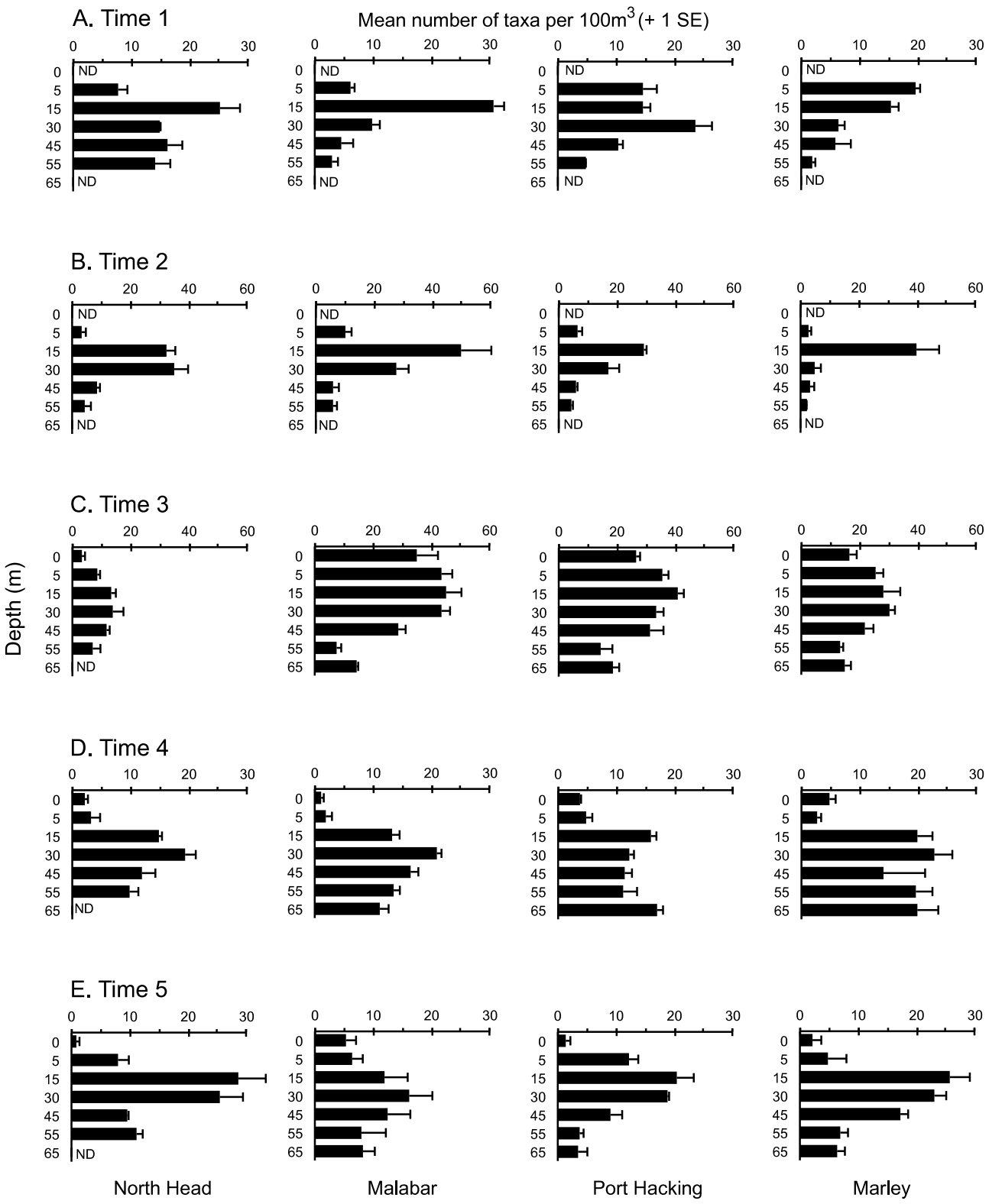

Fig. 2. Mean number (+ 1SE) of identifiable larval fish taxa sampled at each depth across the four sampling stations and five sampling times. ND denotes not sampled.

(i.e. assemblage clusters A versus B and C in Fig. 4). In T1 (except North Head) and T2, there was also discrete separation of assemblage clusters between upper (15–30 m; B) and lower (45–55 m; C) subsurface waters (Fig. 4). Contrasting this, there was no definitive sub-structuring of subsurface assemblages in T3–T5. However, the secondary ordinations of subsurface assemblages in these three times identified an apparent, albeit variable, gradient of change among assemblages from the upper to lower depths (Fig. 4).

The SIMPER analyses identified several taxa that consistently characterized either surface or subsurface assemblages. This included *Acanthopagrus australis* (T2, T3), *Gerres subfasciatus* (T1, T3,

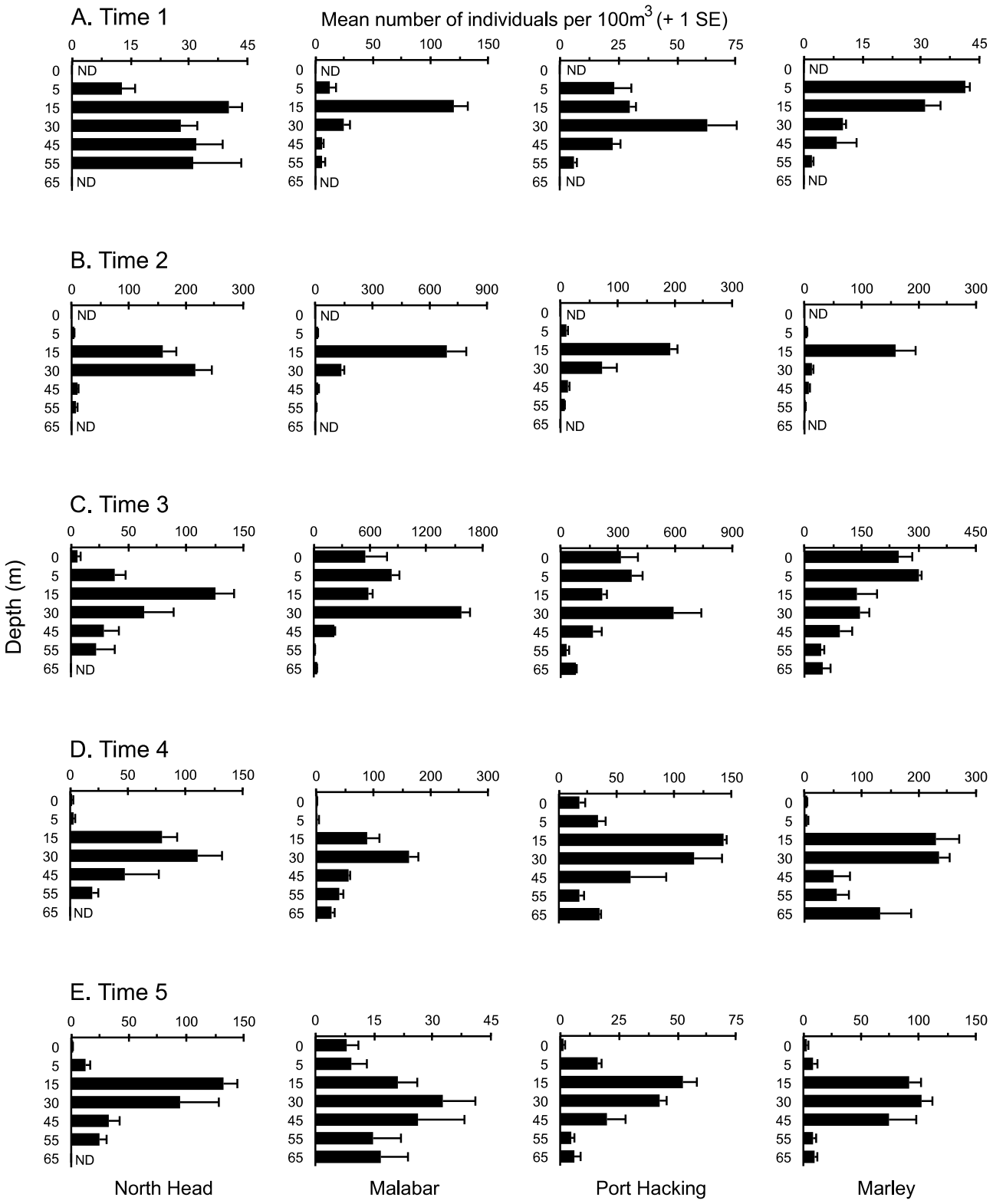

Fig. 3. Mean number (+ 1SE) of individual larval fish sampled at each depth across the four sampling stations and five sampling times. ND denotes not sampled.

T4) and Pomacentridae (T1, T3, T5) in surface assemblages and Triglidae, Platycephalidae, Sillaginidae, Bothidae, Labridae and *Cepola australis* in subsurface assemblages (T1–T5) (Tables 2 and 3). Notably, several taxa contributed greatest to the similarity of the upper and lower subsurface assemblages in T1 and T2; the 10 denoted taxa (except *Cepola australis* in T1) that contributed greatest to the dissimilarity of subsurface assemblage clusters B and C in both T1 and T2 occurred in greater numbers in the upper layer (Table 2).

The total number and the proportion of each individual fish taxa sampled (where the number per taxa sampled was $>$ 20 individuals) at each depth in each sampling time is provided in Supplementary Table 1.

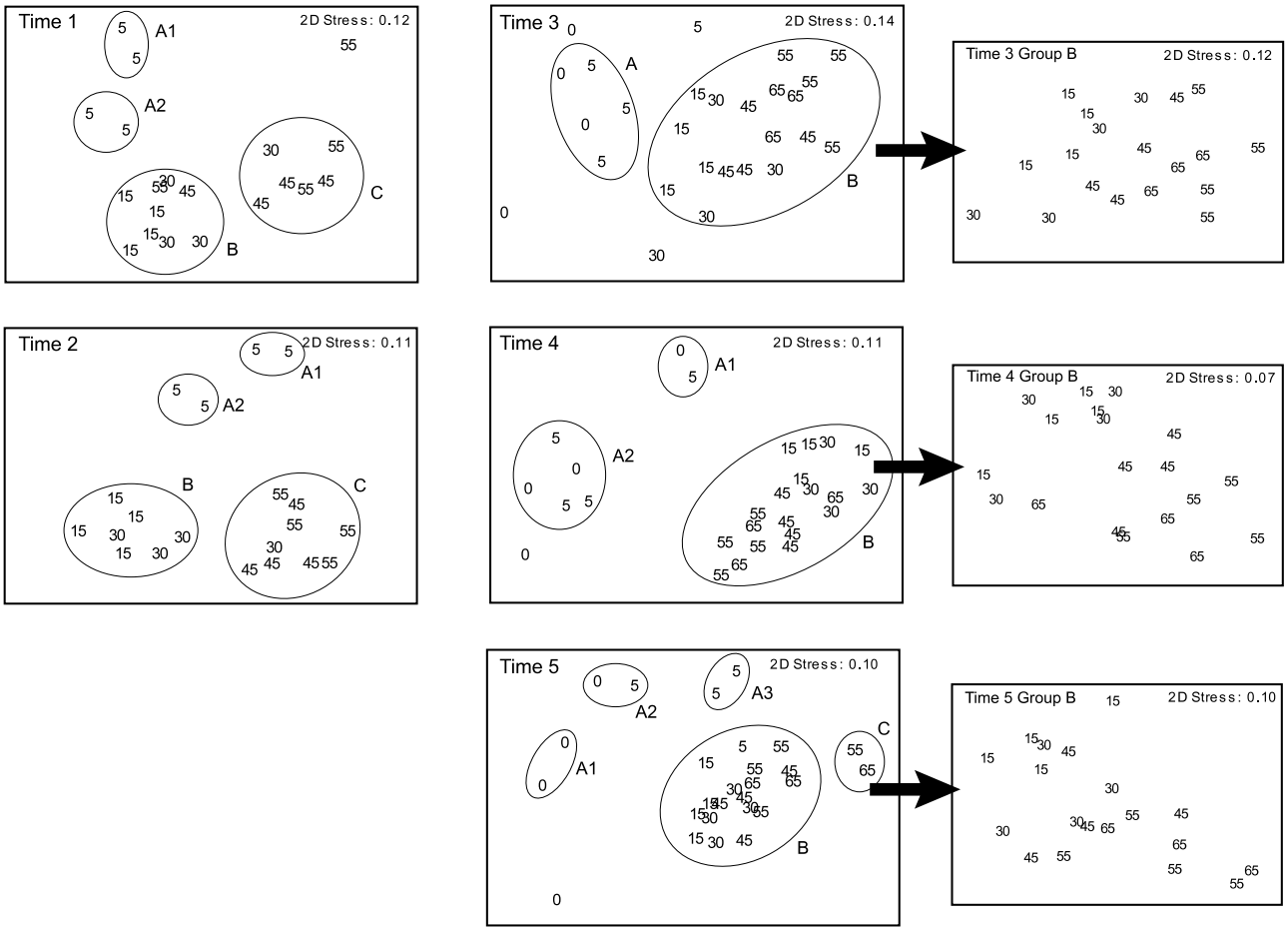

Fig. 4. Nonmetric multidimensional scaling ordination plots displaying depth relationships of larval fish assemblages in each of the five sampling times. The numbers (0 to 65) refer to depth (m) and the letters denote each assemblage grouping as determined by the hierarchical agglomerative Bray–Curtis cluster analysis for each sampling time: A1, A2, A3 refer to surface groups, B and C subsurface groups as referred to in the text and Tables 2 and 3. Secondary ordinations solely of the subsurface assemblages are displayed for Times 3–5.

4. Discussion

All depth strata at times contained abundant and diverse larval fish assemblages, highlighting the importance of the entire water column as a nursery habitat and transport corridor for fish larvae in this coastal zone. Moreover, the larval assemblages included taxa that as adults inhabit oceanic, coastal and estuarine benthic and pelagic environments of tropical and temperate waters, further emphasizing the importance of the broad connectivity of these coastal waters to a wide range of ichthyofauna and as a faunal transition zone (Smith and Suthers, 1999; Gray and Miskiewicz, 2000; Keane and Neira, 2008; Mullaney et al., 2011). It also provides further evidence of the diverse range of ichthyofauna that could be impacted by a shifting regional oceanographic regime resulting from climate-related environmental changes (Hobday and Lough, 2011; Suthers et al., 2011).

Despite evident variation, there was a general trend across sampling times (except T3) for greater numbers of taxa and individuals to be most concentrated in the upper subsurface strata (15–30 m). This is consistent with other complementary historical regional studies (Gray, 1998) and that documented for larval fishes over other continental shelves where most larvae during daylight hours tend to inhabit the upper and mid-water column (Ahlstrom, 1959; Kendall and Naplin, 1981; Boehlert et al., 1985; Rodriguez et al., 2006). Whilst the thermal structure of the water column can be a key determinant in larval fish vertical distributions (Olivar and Sabates, 1997; Höffle et al., 2013), no such relationships have been detected in these current study waters (Gray and Kingsford, 2003) or in similar dynamic oceanographic coastal waters elsewhere (Röpke, 1993; Sabates, 2004; Rodriguez et al., 2006). Rather, it is generally hypothesized that such distributions are a response to prey concentrations and adequate light levels for feeding in upper subsurface waters (Leis, 1991; Gray and Kingsford, 2003; Sabates, 2004; Rodriguez et al., 2006). This hypothesis is further reinforced by observations that larval fish vertical distributions in these (Gray, 1998) and other coastal waters (Brewer and Kleppel, 1986; Haldorson et al., 1993; Sabates, 2004; Rodriguez et al., 2006; Garrido et al., 2009) are more homogeneous throughout the water column at night.

The daytime vertical stratification of the larval fish assemblages could be partitioned into two broad categories: surface (0–5 m) and subsurface (15 m and deeper), with further spatio-temporal sub-structuring of subsurface assemblages into upper (15–30 m) and lower (45–65 m) water column. The apparent sub-structuring of subsurface assemblages was not related to the thermal stratification of the water column (i.e. presence or position of a thermocline); for example, sub-surface assemblages were structured in similar ways in stratified conditions in T3 and T5 and non-stratified conditions in T4. Moreover, vertical stratification of assemblages breaks down at night (Gray, 1998). These observations add further support to the argument that thermoclines are not the primary driver of broad-scale vertical stratification of larval fish assemblages in dynamic coastal waters (Röpke, 1993; Gray and Kingsford, 2003; Sabates, 2004; Rodriguez et al., 2006).

Table 2
Summary of SIMPER analyses listing the 15 taxa that contributed greatest to the similarity matrix of each identified larval fish assemblage group from the cluster analysis for sampling times 1 and 2. Note that for surface assemblages all taxa (i.e. n < 15) that contributed 100% to each similarity matrix is listed. Contribution (%) is the overall contribution of each taxa to the total similarity measure within each grouping; the average similarity is the average contribution of each taxa to the similarity measure across all sample pairs; the similarity/standard deviation ratio is the average similarity divided by the standard deviation of those contributions across all sample pairs; na refers to samples that comprised only two samples and no average similarity/standard deviation ratio could be determined. The annotated numbers (1–10) listed against taxa in Group B are those that contributed greatest to the dissimilarity matrix between assemblage groups B and C.

	Surface					Subsurface — shallow					Subsurface — deep			
	Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation
TIME 1 (February & March 1991)														
Group A1					**Group B**					**Group C**				
Gerres subfasciatus	3.07	40.46	15.95	na	Bothidae[2]	6.02	12.12	6.15	2.41	*Cepola australis*	3.62	40.15	17.97	3.71
Acanthopagrus australis	3.07	35.94	14.17	na	Platycephalidae[5]	7.18	11.26	5.71	2.75	Triglidae	1.08	17.31	7.75	4.12
Myctophidae	0.96	23.6	9.31	na	*Trachurus* spp.[1]	4.75	11.21	5.68	4.28	Callionymidae	0.72	11.59	5.19	1.3
					Triglidae[7]	3.55	11.08	5.62	3.27	Platycephalidae	0.73	10.27	4.6	1.25
					Sillaginidae[3]	3.70	8.77	4.45	1.61	Bothidae	0.31	5.57	2.49	0.77
Group A2					Anguilliformes[6]	2.14	5.77	2.93	1.19	Anguilliformes	0.29	3.16	1.41	0.46
Gerres subfasciatus	6.03	16.06	9.14	na	Trachichthyidae[10]	0.93	4.06	2.06	1.08	Cynoglossidae	0.61	2.54	1.14	0.48
Pomacentridae	6.72	13.52	7.7	na	Cynoglossidae[9]	1.11	3.9	1.98	0.9	Trachichthyidae	0.45	2.42	1.08	0.48
Platycephalidae	2.30	12.43	7.08	na	Labridae	0.48	3.78	1.92	1.66	Gonostomatidae	0.22	1.36	0.61	0.26
Sillaginidae	3.10	12.28	6.99	na	Sciaenidae[8]	1.50	3.24	1.65	0.77	Pempheridae	0.15	1.2	0.54	0.26
Gobiidae	1.77	10.86	6.18	na	Pempheridae	0.93	2.96	1.5	0.92	Moridae	0.26	1.12	0.5	0.26
Acanthopagrus australis	1.03	8.68	4.94	na	Callionymidae	0.57	2.09	1.06	0.76	Sillaginidae	0.24	1.09	0.49	0.26
Petroscirtes lupus	1.24	8.56	4.88	na	*Schuettea scalaripinnis*	0.39	1.86	0.94	0.75	*Schuettea scalaripinnis*	0.15	0.86	0.38	0.26
Pempheridae	0.81	6.16	3.51	na	Aulopidae	0.70	1.82	0.92	0.59	Gobiidae	0.13	0.69	0.31	0.26
Callionymidae	0.77	5.81	3.31	na	*Cepola australis*[4]	0.93	1.61	0.82	0.56	Myctophidae	0.13	0.68	0.31	0.26
Trachurus spp.	1.03	5.63	3.21	na										
	Surface					Subsurface — shallow					Subsurface — deep			
	Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation
TIME 2 (October 1991)														
Group A1					**Group B**					**Group C**				
Girella spp.	0.49	50	16.14	na	Labridae[2]	17.43	10.74	6.64	8.18	*Cepola australis*	3.26	35.15	16.6	4.24
Monacanthidae	0.50	50	16.14	na	Sillaginidae[1]	27.13	9.22	5.7	4.82	Gonostomatidae	1.54	24.82	11.72	1.33
					Cepola australis	18.17	8.12	5.02	1.95	Argentinidae	0.56	12.79	6.04	1.12
Group A2					Triglidae[4]	11.34	7.44	4.6	4.21	Labridae	0.49	5.49	2.59	0.57
Platycephalidae	0.96	17.09	7.37	na	*Sardinops* sp.[6]	11.24	7.18	4.44	3.06	Aulopidae	0.50	5.31	2.51	0.6
Monacanthidae	0.72	16.84	7.27	na	*Engraulis australis*[3]	22.90	7.08	4.38	4.12	Callionymidae	0.36	4.85	2.29	0.6
Acanthopagrus australis	0.48	16.54	7.14	na	Callionymidae[8]	11.15	6.93	4.29	5.36	Myctophidae	0.26	2.79	1.32	0.44
Percophididae	0.48	16.54	7.14	na	*Pseudocaranx* sp.[5]	12.37	5.59	3.45	1.76	Sillaginidae	0.25	2.55	1.21	0.44
Triglidae	0.48	16.54	7.14	na	Platycephalidae[7]	11.76	5.56	3.44	2.35	Moridae	0.17	1.36	0.64	0.3
Engraulis australis	0.49	16.45	7.1	na	Aulopidae	2.60	5.32	3.29	6.18	Anthiinae	0.15	1.26	0.59	0.3
					Creediidae[10]	5.28	5.2	3.22	2.96	*Sardinops* sp.	0.17	1.18	0.56	0.3
					Anthiinae	1.77	3.66	2.26	1.42	*Neosebastes* spp.	0.24	1.18	0.56	0.3
					Bothidae[9]	12.92	3.36	2.08	0.83	*Trachurus* spp.	0.09	0.48	0.23	0.17
					Neosebastes spp.	4.62	3.32	2.05	0.9	Anguilliformes	0.08	0.43	0.2	0.17
					Pomacentridae	2.82	2.22	1.38	0.84	Creediidae	0.09	0.35	0.17	0.17

Table 3
Summary of SIMPER analyses listing the 15 taxa that contributed greatest to the similarity matrix of each identified larval fish assemblage group from the cluster analysis for sampling times 3, 4 and 5. Note that for surface assemblages in Times 4 and 5 all taxa (i.e. n < 15) that contributed 100% to each similarity matrix is listed. Contribution (%) is the overall contribution of each taxa to the total similarity measure within each grouping; the average similarity is the average contribution of each taxa to the similarity measure across all sample pairs; the similarity/standard deviation ratio is the average similarity divided by the standard deviation of those contributions across all sample pairs; na refers to samples that comprised only two samples and no average similarity/standard deviation ratio could be determined.

	Surface					Subsurface			
	Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation
Time 3 (February 1992)									
Group A					**Group B**				
Gerres subfasciatus	81.51	12.83	6.93	4.3	Sillaginidae	24.08	9.7	4.46	2.05
Acanthopagrus australis	105.47	11.74	6.34	8.04	Callionymidae	5.69	7.68	3.53	2.52
Kyphosus sp.	43.58	9.55	5.16	4.52	Platycephalidae	15.47	7.43	3.42	1.79
Pomacentridae	23.46	7.17	3.87	2.23	*Pseudocaranx* sp.	57.97	7.14	3.29	1.65
Schuettea scalaripinnis	14.48	6.4	3.45	3.81	*Cepola australis*	7.69	5.56	2.56	1.14
Seriola sp.	5.47	5.1	2.76	1.66	Triglidae	2.98	5.13	2.36	1.37
Pseudocaranx sp.	2.61	4.15	2.24	2.54	Sciaenidae	14.13	4.53	2.08	1.28
Gonostomatidae	9.93	3.7	2	2.2	Myctophidae	3.00	4.4	2.03	1.12
Liza argentea	9.51	3.23	1.74	1.31	Gobiidae	22.32	4.16	1.91	1.03
Myctophidae	6.78	3.18	1.72	1.24	Gonostomatidae	2.05	3.91	1.8	1
Lophiiformes	1.20	2.86	1.54	2.21	Creediidae	8.34	3.25	1.49	0.98
Mullidae	2.55	2.75	1.49	0.96	Labridae	7.39	3.25	1.49	1.17
Petroscirtes lupus	3.82	2.64	1.42	1.18	*Neosebastes* spp.	4.65	3.09	1.42	0.74
Gonorynchus greyi	29.27	2.57	1.39	0.47	Mugiloididae	2.63	2.28	1.05	0.97
Engraulis australis	4.82	2.06	1.11	1.13	*Engraulis australis*	2.02	2.02	0.93	0.97
Sillaginidae	24.75	1.78	0.96	0.48	Anguilliformes	3.70	1.98	0.91	0.64
Pempheridae	8.14	1.59	0.86	0.76	*Apogonops anomalus*	2.95	1.75	0.8	0.49
Girella tricuspidata	5.33	1.57	0.85	0.67	Bothidae	1.21	1.55	0.71	0.68
Platycephalidae	7.42	1.42	0.76	0.69	*Centroberyx affinis*	3.32	1.49	0.69	0.64
Gobiidae	7.15	1.31	0.71	0.78	*Schuettea scalaripinnis*	2.59	1.45	0.67	0.61
	Surface					Subsurface			
	Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation
Time 4 (August & September 1992)									
Group A1					**Group B**				
Macrorhamphosus spp.	9.34	55.12	22.8	2.59	Myctophidae	5.76	12.15	6.64	3.9
Sardinops sp.	0.60	31.54	13.05	1.05	Bothidae	22.33	10.25	5.6	1.61
Anthiinae	0.46	8.28	3.42	0.61	*Sardinops* sp.	13.80	9.95	5.43	2
Myctophidae	0.55	2.97	1.23	0.32	*Pseudocaranx* sp.	15.54	9.63	5.26	1.34
Scorpididae	0.18	2.09	0.86	0.32	*Helicolenus* spp.	5.06	7.53	4.11	1.84
					Triglidae	2.22	6.51	3.56	1.71
Group A2					Moridae	3.08	6.2	3.38	1.93
Scorpididae	0.72	28.54	15.38	na	Trichiuridae	2.66	5.77	3.15	1.04
Monacanthidae	1.01	24.72	13.32	na	*Cepola australis*	3.61	5.22	2.85	0.99
Liza argentea	0.61	23.37	12.6	na	Callionymidae	1.22	4.09	2.23	1.36
Sardinops sp.	0.99	23.37	12.6	na	*Macrorhamphosus* spp.	3.41	2.97	1.62	0.67
					Gonostomatidae	0.81	2.91	1.59	0.99
					Hoplichthys spp.	0.73	2.76	1.51	0.97
					Anthiinae	1.31	2.13	1.17	0.85
					Carapidae	0.63	1.68	0.92	0.74
					Labridae	1.26	1.6	0.88	0.61
					Callanthiinae	0.87	1.46	0.8	0.56
					Platycephalidae	0.52	1.34	0.73	0.66
					Argentinidae	0.39	1.01	0.55	0.4
					Sillaginidae	0.50	0.77	0.42	0.42
					Mugiloididae	0.37	0.71	0.39	0.41
					Scomber spp.	0.44	0.52	0.28	0.36

(*continued on next page*)

Differences in daytime assemblage structure between surface and subsurface waters were primarily driven by several species that predominantly occurred in one depth zone and not the other. Notably, a small suite of taxa was characteristic and abundant in surface waters but not in subsurface waters, including *G. subfasciatus*, *A. australis*, *Gonorynchus greyi*, *Macrorhamphosus* spp., Mullidae and Scorpididae, which is consistent with other broader scale regional studies (Gray and Miskiewicz, 2000). In contrast, most taxa that occurred in subsurface waters displayed broad depth distributions (5–65 m). Moreover, most taxa were not consistently concentrated in either upper or deeper depths and depth-associated changes in densities often graduated across several depths. Differences in assemblage structure between upper and lower subsurface waters was therefore mostly driven by taxa common to both zones but occurring in differing densities across certain depth strata. In T1 and T2 most discriminating taxa were more abundant in upper compared to lower subsurface

Table 3 (*continued*).

	Surface					Subsurface			
	Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation		Mean number 100 m^3	Contribution %	Average similarity	Similarity/ standard deviation
Time 5 (November & December 1992)									
Group A1					**Group B**				
Dactylopterus spp.	0.50	100	35.03	na	Callionymidae	3.90	13.07	5.85	1.97
					Sillaginidae	3.79	10.43	4.67	2.02
Group A2					*Neosebastes* spp.	2.36	8.61	3.86	1.54
Dactylopterus spp.	1.39	39.58	14.92	na	Triglidae	1.99	7.65	3.43	1.38
Pelates quadrilineatus	2.22	36.07	13.6	na	Creediidae	5.62	7.01	3.14	0.94
Macrorhamphosus spp.	1.74	24.35	9.18	na	Platycephalidae	4.17	6.91	3.09	1.22
					Cepola australis	1.01	5.5	2.46	1.03
Group A3					*Sardinops* sp.	1.81	4.51	2.02	0.94
Pomacentridae	1.50	20.62	9.11	na	Mugiloididae	1.15	4.28	1.92	0.82
Platycephalidae	1.03	12.37	5.47	na	*Engraulis australis*	2.04	4.18	1.87	1.05
Acanthopagrus australis	2.36	11.66	5.15	na	Labridae	0.97	3.6	1.61	0.78
Labridae	0.72	11.66	5.15	na	*Pseudocaranx* sp.	4.45	3.41	1.53	0.69
Gerres subfasciatus	0.78	11.06	4.89	na	Bothidae	1.14	2.96	1.33	0.79
Pseudocaranx sp.	0.52	10.9	4.82	na	Gobiidae	0.90	2.08	0.93	0.54
Pseudorhombus spp.	0.51	10.88	4.81	na	*Pseudorhombus* spp.	1.28	2.02	0.91	0.65
Sillaginidae	0.51	10.88	4.81	na	Percophididae	1.09	1.73	0.77	0.55
					Argentinidae	0.50	1.59	0.71	0.43
					Pomacentridae	0.38	1.4	0.63	0.49
					Centropogen australis	0.81	1.29	0.58	0.44
					Moridae	0.79	1.08	0.48	0.31
					Myctophidae	0.36	0.99	0.44	0.36
					Group C				
					Argentinidae	1.38	34.41	20.73	na
					Mugiloididae	1.31	28.57	17.21	na
					Gonostomatidae	0.37	13.81	8.32	na
					Cepola australis	0.42	11.61	6.99	na
					Triglidae	0.39	11.61	6.99	na

waters, but such distribution and abundance patterns were not consistent being variable in space and time over small and large scales and among taxa. Therefore, delineations among upper and lower assemblages were fluid and not consistent, with more subtle depth-associated changes in assemblage structures observed. Flexible vertical distributions of individual taxa and assemblage structuring could be a mechanism that facilitates resource partitioning (Leis, 1991).

Since this study was done there have been no comparative similar-scaled vertically-stratified sampling studies of larval assemblages in the region. More recent studies have primarily examined broad-scale horizontal patterns of assemblages associated with the presence and movements of different water masses along and across the continental shelf in deeper and more offshore waters than sampled here (Smith et al., 2016). Moreover, such studies have mostly utilized oblique sampling strategies across much broader-scale depth strata than done here.

In summary, this historical study demonstrated consistency in vertical stratification between surface and subsurface larval fish assemblages in southeast Australian coastal waters, and that further sub-structuring of subsurface assemblages was spatially and temporally variable and not related to thermal stratification of the water column. Rather, other factors such as prey concentrations and light levels along with small-scale currents probably play an integral role in the vertical structuring of larval fish assemblages in coastal waters (Gray and Kingsford, 2003; Sabates, 2004; Rodriguez et al., 2006).

Similar to regional studies elsewhere (e.g. Tsikopoulou et al., 2019), the historical data provided here and in other complementary regional ichthyoplankton studies (see Smith et al., 2016, 2018) can be used as a benchmark in future assessments of anthropogenic- and climate-related environmental impacts on marine ecosystem structure and function in this dynamic coastal region.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2019.100634.

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